Asian Journal of
Plant Sciences

Multi-scale Ecological Adaptation of a Young Mixed Broadleaved and Coniferous Korean Pine Forest Community to Drought

[1,2]Xiongwen Chen, [2]Guangsheng Zhou and [1]Bai-Lian Li
[1]Department of Botany and Plant Sciences,
University of California, Riverside, CA 92521-0124, USA
[2]Laboratory of Quantitative Vegetation Ecology, Institute of Botany,
Chinese Academy of Sciences, Beijing, 100093, P.R. China

Abstract: The multi-scale mechanisms of how communities or ecosystems adapt to drought are important for natural resources management and developing mitigation strategies under global climatic change. We studied the adaptive response from different scales of a young mixed broadleaved and coniferous Korean pine forest community (YMBCKPFC) under temporary water limitation or drought in Northeast China. YMBCKPFC acclimated to water limitation, or drought pulse, from community scale to plant species and plant leaves. Leaf water content and water potential were lower for most plant species at water limitation. For all species the leaf evapotranspiration increased and stomatal conductance decreased. Photosynthetic rates of many species decreased first and then increased, but others continue to increase their photosynthetic rates. Most species adapted to water limitation by decreasing their growth rate. Fruits of *Rosa suavis* became mature earlier under drought conditions. Soil respiration increased as the soil water content decreased. The total water consumption of YMBCKPFC decreased slightly under water limitation. The spatially heterogeneous distribution of soil water was advantageous for YMBCKPFC to adapt to water limitation. The contents of soil nutrients changed under drought condition. Soil P decreased and soil K increased, but the change of soil total C, N and S seemed complicated. Functional convergence and divergence of basic physiological processes existed while YMBCKPFC adapted to drought at multi-scales. The functional divergence or response diversity may be helpful to the survival and succession of this community.

Key words: Adaptation, drought, leaf physiological parameters, multi-scale, mixed broadleaved coniferous Korean pine forest, soil water, nutrient

INTRODUCTION

Increased air temperature and drought in Northeast China is a consistent prediction of general circulation models based on increasing greenhouse warming scenarios[1-5]. In fact, the air temperature has increased 1.2°C during the last 40 years in Northeast China[6,7]. During the last 40 years at the area of north of 35°N in China the air temperature increased about 0.24°C every decade and it likely will continue to increase[8]. Furthermore, underground water table is decreasing, because of overuse of groundwater for local industrial and agricultural development and decreased precipitation due to global climate change and local environmental change. Therefore, drought is inevitable in Northeast China, where the largest and most important forest region in China is located. In fact, sporadic and prolonged drought has often occurred in this area.

The possible effects of climate change on the main forest ecosystems in this area have been reported[9,10] and research on evapotranspiration of several tree species under drought condition indicated that different tree species could adapt to different drought conditions[11]. However, the mechanism of how a natural forest community or ecosystem adapts to drought remains unclear. Recent research indicated that there is functional convergence in plant responses to the environment[12]. Characterizing the trade-offs that individual species operate at multiple scales will enhance understanding of the adaptation and resistance of a community and ecosystem to drought. This is necessary in order to adapt to climatic change and mitigate social and economical loss. The results of separated plant species or several co-occurring species to drought can not be directly expanded to the community or ecosystem level; also the research in controlled-climate laboratory can not completely represent

Corresponding Author: Xiongwen Chen, Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124, USA Tel: 909-787-4776 Fax: 909-787-4437 E-mail: xchen@citrus.ucr.edu

the natural ecosystem. The need for investigations into the ecological response of forest communities or ecosystems to drought in natural conditions is urgent. Numerous quick-response mechanisms and feedback loops are created within the community or ecosystem to enhance overall stability[13]. Therefore, the aim of our research is to study the mechanism of a typical young mixed broadleaved and coniferous Korean pine forest community (YMBCKPFC) to adapt to water limitation or a temporary drought in natural conditions. The present analysis was conducted at multiple scales and included: 1) adaptation of community variables under temporary drought, including soil water, respiration and nutrients; 2) adaptation of plant species, including species growth, composition and phenology; 3) adaptation of plant leaves to drought, including leaf water content, water potential and photosynthesis and 4) a test of functional convergence or divergence theory based on the species responses at multi-scale.

MATERIALS AND METHODS

Study area and plant community: After a long period of clear cutting, Northeast China is now dominated by young secondary forests. This research was carried out in a YMBCKPFC, succeeded from a clear cut. The location of the experimental site is 42°24'7.7"N, 128°5'45"E and at an elevation of 500 m. It is near the Long Term Ecological Station at Changbai Mountain of Chinese Academy of Sciences. The climate of Changbai Mountain is characterized by long cold winters and short cool summers. The annual mean temperature in the study area ranges from -7 to 3°C and the annual average precipitation ranges from 700 to 1400 mm[14]. The age of the forest stand is 5 years. The slope is less than 2 degrees. The main plant species of this young forest are *Acer mono, Quercus mongolica, Betula platylla, Tilia amurensis, Ulmus propinqua, Populus* spp., *Salix* spp., *Pinus koraiensis, Larix olgensis, Picea jezoensis, Lonicera caerulea* var. edulis, *Lonicera ruprechtiana, Rosa suavis, Evony pauciflorus, Viburnum sargentii, Padus racemosa, Cerasus maximowiczii* and *Phegopteris polypodioides.* The stand has regenerated naturally and the stand height is about 3.0 m. It is at an early stage of the secondary succession. The coniferous species are lower in stature than the broadleaved tree species. The stand has closed canopy because of the dense seedlings. This kind of young forest grows fast and develops toward mature mixed coniferous and broadleaved forest.

The experiment was carried out on two adjoining plots and each was 6×6 m². Plant communities at these two plots were similar. The species name, height and stem

diameter at 2 cm height were recorded for each plant individual on both plots at the beginning and end of the experiment. Soil samples at different depths (10, 20, 60 cm) at three time period (8:00, 12:00 and 18:00) were obtained to measure soil nutrients. The diurnal photosynthesis rate of main species was measured. On June 24, 2001 along the boundaries of one plot (Plot 1) hard plastic sheets were inserted at the soil depth of 1.0 m and 10 cm above ground so that surface ground water (10 cm) and underground water (<1.0 m) could not enter this plot; the plant community was also covered by transparent plastic material at the height of 5.0 m at night and the rain time during the experiment in order to prevent moisture and rain from entering the community. The adjoining plot (Plot 2) was used for control comparison.

Plant photosynthesis: Net photosynthesis, transpiration and stomatal conductance of each species in both plots were measured simultaneously. Six randomly chosen leaves at the top or near top of each species were measured every 2 h from 8 a.m. to 6 p.m. in the beginning and during the experiment by LCi Portable Photosynthesis System (ADC BioScientific CO., UK).

Soil water and nutrients: In order to avoid large variance of soil water content, four locations within 10 cm of each other were chosen in each plot. At each location soil samples (>100 g) were collected at every 10 cm depth from 0 to 100 cm, every 2 h from 8 a.m. to 4 p.m. All the soil samples were put into seized plastic bags immediately. Later, the soil water contents of samples were estimated after 14 h in 105°C. Soil bulk densities were measured at depths of 5, 20, 70 cm on a profile. Soil samples (>200 g) were obtained at the depth of 0-10, 10-30, 30-100 cm to analyze soil nutrients by standard procedures: the total content of C in soil samples was analyzed by LECO SC444. Organic carbon was calculated as total carbon minus $CaCO_3$ (Scheibler). Because of the limited content of $CaCO_3$, organic carbon is called total C in this study; total N was measured by Kjeldahl; K, P and S were measured by ICPS (inductive coupled plasma spectrometry) after digestion with HNO/ HCLO. In this study the total water stock (W_t, g cm^{-2}) was calculated as following[55]:

$$W_t = BDxC_c\%xD$$

Where BD is soil bulk density (g cm^{-3}); $C_c\%$ is soil water content and D is soil sampling depth (cm).

Leaf water content: Leaf water content was estimated by the following:

leaf water content = (leaf wet weight- leaf dry weight)/leaf area

Leaf wet weight was measured in the morning (about 7:00 am). Leaf area was measured by AM200 portable leaf area measurer (ADC BioScientific Ltd.). For each plant species 10 random leaves near top were measured. Leaf dry weight was measured after the leaves were oven-dried for 24 h at 97°C.

Leaf water potential: Pre-dawn (4:00-5:00 am) leaf water pressures were measured for each plant species in a pressure chamber as described by Turner[15] on 4 leaves of the fully expanded leaves at the same height.

Soil respiration: Soil respiration was measured by LICOR 6200 portable photosynthesis system (LICOR, Inc., Lincoln, NE) at every 2 h from 8 a.m. to 6 p.m. in both plots and at each time soil CO_2 fluxes were monitored for four consecutive times.

Plant phenology: Plant phenology was monitored by the fruits of *Rosa suavis*. When its fruits were mature, their color turned into red. We measured the percentage of matured fruits after we collected all fruits in both plots on July 12, 2001.

RESULTS

Soil water content change: In Plot 1 the soil water content at lower soil horizons and total water consumption decreased. Diurnal averages of the soil water content at each 10 cm, from soil surface to 100 cm depth, were similar on both plots at the beginning of the experiment (Table 1). After one week the soil water contents at different depths in both plots were not significantly different. However, after two weeks, the difference of soil water content occurred mainly at depths of 10-40 cm. After about 3 weeks, Plot 1 had lower soil water content from the surface to about 40 cm depth. Total water loss in Plot 1 was similar with Plot 2 from June 24 to July 12, but Plot 2 received more water than Plot 1 (Table 2). In order to adapt to decreasing water supply there was slight difference in soil water input and uptake between Plot 1 and Plot 2. Soil received water mainly at depths of 30-40 and 80-100 cm in Plot 1, but for Plot 2 water input occurred at the soil surface, 20-40 and 80-100 cm depth. In Plot 1 water uptake occurred mainly at 0-20 and 50-70 cm depth, but uptake occurred mainly at 0-30 and 50-80 cm depths in Plot 2.

Soil nutrient change: In Plot 1 soil C content decreased more than that in Plot 2 during the experiment period (Table 3). Soil N content increased first but decreased at Plot 1 on July 12; however, it continued to increase at Plot 2. Soil P and K were sensitive and changed obviously under water limitation. Soil P decreased on July 12, but soil K increased continually at Plot 1. The change of soil S content was similar with that of soil C.

Soil respiration rate: Soil respiration rate in Plot 1 was higher than that in Plot 2 (Table 4). Soil respiration increased significantly as the soil water content decreased. But their regression relationship was not significant.

Water content change in plant leaves: Water content of plant leaves was sensitive to soil water content change. On July 7 the average soil water content at the horizon of 100 cm in Plot 1 only decreased slightly compared with those on June 24, but leaves of plant species decreased their water content dramatically (Table 5). Leaf water contents were higher for the main species on Plot 2 for the increased soil water content. *A. mono, Q. mongolica, T. amurensis, P. davidiana, C. maximowiczii, B. platyphylla, P. polypodioides* and *P. koraiensis* were sensitive in their leaf water contents. The leaf water potentials of most plant species in Plot 1 were lower than those in Plot 2 because the soil water content in Plot 1 was lower than that of Plot 2, except for *Salix, R. suavis, B. platyphylla* and *Picea koraiensis.*

Leaf photosynthetic rate: The change of photosynthetic rate of main plant species was complicated under natural conditions because air temperature, PAR (photosynthetic available radiation) and soil water content all affected photosynthesis. However, for all species the leaf evapotranspiration increased and stomatal conductance decreased. Two groups of plant species could be classified depending on the photosynthetic rates. 1) Many species decreased their photosynthetic rates first and then increased, such as *Q. mongolica* (Table 6) and some even increased their photosynthetic rate dramatically, such as *L. olgensis, Picea koraiensis* and *P. koraiensis;* and 2) some species continued to increase their photosynthetic rates, such as *R. suavis* (Table 6).

Plant growth: For most species the growth rates in height and stem diameter decreased in Plot 1 in comparison with those in Plot 2 (Table 7). However, for *A. mono* and *Picea koraiensis* in Plot 1 the growth rate in height and stem diameter was slightly higher than the same species in Plot 2, respectively; for *Q. mongolica* the height growth rate was slightly higher than the same species in Plot 2.

Table 1: The diurnal soil water content (gg^{-1}) at different soil depths in both plots

Soil depths (cm)	June 24 Plot 1	Plot 2	June 29 Plot 1	Plot 2	July 7 Plot 1	Plot 2	July 12 Plot 1	Plot 2
0	0.485(±0.069)	0.496(±0.075)	0.643(±0.053)	0.585(±0.041)	0.661(±0.104)	0.673(±0.074)	0.473(±0.103)	0.563(±0.100)
10	0.312(±0.169)	0.351(±0.053)	0.391(±0.024)	0.356(±0.040)	0.344(±0.043)	0.466(±0.062)	0.299(±0.074)	0.342(±0.064)
20	0.192(±0.030)	0.203(±0.055)	0.192(±0.033)	0.164(±0.007)	0.185(±0.012)	0.276(±0.074)	0.181(±0.010)	0.284(±0.041)
30	0.182(±0.035)	0.201(±0.011)	0.180(±0.031)	0.183(±0.005)	0.182(±0.025)	0.247(±0.028)	0.224(±0.043)	0.247(±0.035)
40	0.170(±0.008)	0.184(±0.023)	0.172(±0.019)	0.191(±0.019)	0.166(±0.012)	0.209(±0.022)	0.183(±0.020)	0.214(±0.028)
50	0.200(±0.013)	0.201(±0.036)	0.172(±0.018)	0.191(±0.018)	0.181(±0.021)	0.197(±0.019)	0.184(±0.032)	0.199(±0.017)
60	0.186(±0.019)	0.183(±0.041)	0.173(±0.015)	0.190(±0.017)	0.180(±0.011)	0.192(±0.011)	0.181(±0.012)	0.185(±0.009)
70	0.180(±0.025)	0.194(±0.014)	0.175(±0.014)	0.205(±0.026)	0.201(±0.040)	0.196(±0.011)	0.188(±0.012)	0.210(±0.016)
80	0.168(±0.012)	0.189(±0.016)	0.177(±0.014)	0.219(±0.030)	0.189(±0.012)	0.192(±0.024)	0.194(±0.018)	0.192(±0.016)
90	0.181(±0.070)	0.167(±0.016)	0.179(±0.014)	0.209(±0.019)	0.193(±0.014)	0.200(±0.010)	0.203(±0.007)	0.206(±0.011)
100	0.182(±0.022)	0.179(±0.016)	0.181(±0.013)	0.195(±0.009)	0.187(±0.016)	0.204(±0.011)	0.218(±0.010)	0.217(±0.019)

Note: values in ( ) are standard deviations.

Table 2: The average quantities of obtained and lost water (kg) in both plots from June 24 to July 12 at different soil depths

		0 cm	10 cm	20 cm	30 cm	40 cm	50 cm	60 cm	70 cm	80 cm	90 cm	100 cm	Total
Plot 1	Obtained	332.457	149.395	1.626	243.539	101.647	66.766	47.426	145.912	148.283	132.612	213.062	1582.730
		(±30.156)	(±14.510)	(±0.165)	(±19.874)	(±10.695)	(±5.983)	(±4.001)	(±13.869)	(±13.968)	(±14.652)	(±20.954)	(±150.231)
	Lost	354.158	173.575	62.207	7.379	30.000	160.314	75.697	103.818	0.298	10.497	2.87	980.521
		(±31.210)	(±17.351)	(±5.896)	(±0.569)	(±2.958)	(±14.985)	(±6.958)	(±9.521)	(±0.096)	(±0.962)	(±0.153)	(±100.235)
Plot 2	Obtained	333.148	207.338	217.624	234.446	676.901	220.140	359.723	98.949	173.412	0.125	49.183	59.090
		(±30.159)	(±21.682)	(±21.671)	(±21.524)	(±60.187)	(±21.364)	(±33.256)	(±9.356)	(±15.698)	(±0.098)	(±4.102)	(±6.021)
	Lost	51.293	35.482	140.738	47.534	175.579	157.381	271.872	46.699	220.129	0.152	2669.601	1107.060
		(±5.962)	(±3.215)	(±13.256)	(±3.012)	(±16.953)	(±14.980)	(±26.391)	(±5.987)	(±20.356)	(±0.052)	(±280.621)	(±100.235)

Note: values in ( ) are standard deviations.

Table 3: Average soil nutrient concentrations (%) of C, N, P, K and S at different depths in both plots from June 24 to July 12

Time	Plot	0 cm C	N	P	K	S	30 cm C	N	P	K	S
June 24	Plot 1	22.943	1.715	0.142	1.123	0.428	0.591	0.135	0.091	1.830	0.017
		(±1.201)	(±0.062)	(±0.005)	(±0.124)	(±0.021)	(±0.061)	(±0.014)	(±0.003)	(±0.064)	(±0.001)
	Plot 2	13.827	1.194	0.108	1.598	0.254	0.433	0.118	0.074	2.892	0.012
		(±0.748)	(±0.051)	(±0.004)	(±0.152)	(±0.012)	(±0.042)	(±0.011)	(±0.002)	(±0.072)	(±0.001)
June 29	Plot 1	12.084	1.859	0.147	1.617	0.329	0.749	0.149	0.106	2.774	0.023
		(±0.721)	(±0.058)	(±0.005)	(±0.156)	(±0.013)	(±0.071)	(±0.013)	(±0.002)	(±0.054)	(±0.001)
	Plot 2	10.687	1.541	0.136	1.688	0.315	0.746	0.132	0.097	2.716	0.022
		(±0.743)	(±0.055)	(±0.005)	(±0.151)	(±0.013)	(±0.072)	(±0.014)	(±0.001)	(±0.062)	(±0.001)
July 7	Plot 1	21.530	2.006	0.153	1.701	0.416	0.888	0.155	0.102	2.829	0.027
		(±0.623)	(±0.050)	(±0.006)	(±0.156)	(±0.021)	(±0.081)	(±0.016)	(±0.003)	(±0.071)	(±0.001)
	Plot 2	19.043	1.771	0.137	1.831	0.355	0.783	0.148	0.092	2.705	0.023
		(±0.942)	(±0.058)	(±0.004)	(±0.162)	(±0.015)	(±0.084)	(±0.014)	(±0.002)	(±0.062)	(±0.001)
July 12	Plot 1	7.847	0.872	0.102	2.182	0.150	0.521	0.126	0.055	2.909	0.014
		(±0.834)	(±0.057)	(±0.003)	(±0.159)	(±0.012)	(±0.052)	(±0.013)	(±0.003)	(±0.084)	(±0.001)
	Plot 2	18.077	1.796	0.126	1.762	0.329	1.287	0.153	0.042	2.829	0.038
		(±0.789)	(±0.048)	(±0.005)	(±0.148)	(±0.012)	(±0.132)	(±0.016)	(±0.003)	(±0.092)	(±0.001)

Time	Plot	60 cm C	N	P	K	S	100 cm C	N	P	K	S
June 24	Plot 1	0.503	0.120	0.071	2.445	0.015	0.422	0.093	0.048	2.273	0.012
		(±0.052)	(±0.010)	(±0.002)	(±0.032)	(±0.001)	(±0.041)	(±0.012)	(±0.002)	(±0.014)	(±0.001)
	Plot 2	0.357	0.095	0.051	2.419	0.009	0.247	0.082	0.035	2.292	0.008
		(±0.031)	(±0.012)	(±0.003)	(±0.021)	(±0.001)	(±0.024)	(±0.014)	(±0.002)	(±0.013)	(±0.001)
June 29	Plot 1	0.514	0.122	0.072	2.512	0.023	0.254	0.106	0.057	2.340	0.011
		(±0.053)	(±0.010)	(±0.002)	(±0.020)	(±0.001)	(±0.021)	(±0.010)	(±0.002)	(±0.010)	(±0.001)
	Plot 2	0.516	0.113	0.065	2.394	0.014	0.357	0.098	0.051	2.251	0.010
		(±0.050)	(±0.011)	(±0.001)	(±0.025)	(±0.001)	(±0.029)	(±0.008)	(±0.002)	(±0.011)	(±0.001)
July 7	Plot 1	0.549	0.130	0.074	2.594	0.017	0.379	0.103	0.046	2.384	0.011
		(±0.054)	(±0.012)	(±0.002)	(±0.021)	(±0.002)	(±0.041)	(±0.013)	(±0.001)	(±0.013)	(±0.001)
	Plot 2	0.494	0.121	0.065	2.487	0.015	0.346	0.094	0.040	2.276	0.010
		(±0.046)	(±0.01)	(±0.002)	(±0.024)	(±0.002)	(±0.032)	(±0.011)	(±0.001)	(±0.014)	(±0.001)
July 12	Plot 1	0.361	0.109	0.045	2.666	0.010	0.255	0.095	0.039	2.423	0.008
		(±0.029)	(±0.007)	(±0.003)	(±0.019)	(±0.002)	(±0.031)	(±0.014)	(±0.001)	(±0.012)	(±0.001)
	Plot 2	0.357	0.116	0.044	2.733	0.012	0.202	0.102	0.038	2.426	0.009
		(±0.048)	(±0.018)	(±0.002)	(±0.022)	(±0.002)	(±0.02)	(±0.013)	(±0.001)	(±0.0012)	(±0.001)

Note: values in ( ) are standard deviations.

Table 4: Diurnal soil respiration (µmol m^{-2} s^{-1}) in both plots

Time	8:00	10:00	12:00	14:00	16:00	18:00
Plot 1	249.67 (±19.04)	194.25 (±44.24)	162.25 (±43.22)	189.32 (±63.01)	208.67 (±14.24)	138.26 (±8.74)
Plot 2	56.75 (±24.13)	53.23 (±10.41)	55.33 (±2.41)	55.05 (±1.23)	75.33 (±2.04)	59.33 (±27.34)

Note: values in ( ) are standard deviations.

Table 5: Leaf water content (%) and water potential (Bar/22.5°C) in main plant species at both plots on June 24 and July 7

Plot	Time	A. mono	Q. mongolica	T. amurensis	P. davidiana	C. maximowiczii	Salix spp.	
Plot 1	June 24	0.1746	0.1483	0.2581	0.0817	0.08167	0.0313	
		(0.002)	(0.0019)	(0.0025)	(0.0042)	(0.0041)	(0.0016)	
	July 7	0.0113	0.0085	0.0146	0.0032	0.0073	0.0069	
		(0.0018)	(0.0009)	(0.0021)	(0.0011)	(0.0012)	(0.0005)	
	WP	-19.07	-18.6	-22.3	-20.63	-20.63	-21.30	
		(0.10)	(0.09)	(0.08)	(0.06)	(0.08)	(0.09)	
Plot 2	June 24	0.0099	0.0101	0.0110	0.0041	0.0102	0.0055	
		(0.0011)	(0.005)	(0.0012)	(0.0019)	(0.0082)	(0.0091)	
	July 7	0.0120	0.0113	0.0167	0.0109	0.0132	0.0091	
		(0.0005)	(0.0039)	(0.0014)	(0.0022)	(0.0046)	(0.0009)	
	WP	-17.33	-18.47	-17.67	-19.87	-19.87	-21.33	
		(0.08)	(0.07)	(0.09)	(0.05)	(0.03)	(0.10)	
		R. suavis	E. pauciflorus	B. platyphylla	P. polypodioides	P. koraiensis	P. koraiensis	L. olgensis
Plot 1	June 24	0.0145	0.0531	0.1071	0.2550	0.1271	0.2550	0.083
		(0.0008)	(0.0026)	(0.0032)	(0.0026)	(0.0081)	(0.0081)	(0.004)
	July 7	0.0034	0.0133	0.0113	0.0170	0.0152	0.0170	0.0103
		(0.0006)	(0.0011)	(0.0051)	(0.0026)	(0.0024)	(0.0009)	(0.0021)
	WP	-23.94	-19.90	-23.37	-17.87	-18.76		
		(0.07)	(0.1)	(0.06)	(0.2)	(0.08)		
Plot 2	June 24	0.0034	0.013	0.0109	0.0083	0.0132	0.0296	0.0137
		(0.0021)	(0.002)	(0.0028)	(0.0013)	(0.0098)	(0.0011)	(0.0025)
	July 7	0.0056	0.0115	0.0068	0.0125	0.0205	0.0313	0.0215
		(0.0007)	(0.0018)	(0.0009)	(0.001)	(0.0041)	(0.0022)	(0.0021)
	WP	-26.73	-20.03	-18.50	-21.23	-20.17		
		(0.08)	(0.07)	(0.11)	(0.05)	(0.09)		

* WP: water potential of leaves. Values in ( ) are standard deviations.

Table 6: The average diurnal photosynthetic rate (µmol m^{-2} s^{-1}) of *Q. mongolica* and *R. Suavis*

	June 24		June 29		July 7	
	Plot 1	Plot 2	Plot 1	Plot 2	Plot 1	Plot 2
Q. mongolica	24.49 (±2.04)	11.91 (±1.14)	9.79 (±1.22)	10.30 (±1.04)	19.29 (±2.44)	42.54 (±3.41)
R. Suavis	4.40 (±1.42)	7.70 (±1.08)	6.42 (±1.04)	5.84 (±0.98)	10.25 (±1.32)	26.42 (±2.2)

Note: values in ( ) are standard deviations.

Table 7: Increments of height and stem diameter for the main plant species in Plot 1 and Plot 2

Plot		Salix spp.	Q. mongolica	E. pauciflorus	L. ruprechtiana	A. mono	P. koraiensis	R. suavis	T. amurensis	B. platyphylla	Picea koraiensis
Plot 1	Increment of average height (cm)	16.502 (±0.52)	2.511 (±0.27)	5.101 (±0.16)	7.830 (±0.300)	0.806 (±0.120)	0.202 (±0.020)	2.175 (±0.050)	0.621 (±0.09)	12.8 (±0.120)	3.02 (±0.250)
	Increment of average stem diameter (cm)	0.107 (±0.052)	0.271 (±0.082)	0.001 (±0.001)	0.110 (±0.020)	0.131 (±0.019)	0.028 (±0.025)	0.025 (±0.011)	0.130 (±0.002)	0.112 (±0.008)	0.08 (±0.010)
Plot 2	Increment of average height (cm)	33.870 (±0.63)	1.302 (±0.50)	5.281 (±0.180)	25.201 (±0.190)	0.411 (±0.200)	0.250 (±0.030)	3.270 (±0.040)	10.251 (±0.021)	24.210 (±0.080)	1.00 (±0.170)
	Increment of average stem diameter (cm)	0.361 (±0.063)	0.410 (±0.019)	0.240 (±0.004)	0.220 (±0.030)	0.089 (±0.017)	0.021 (±0.002)	0.136 (±0.024)	0.133 (±0.002)	0.110 (±0.007)	0.031 (±0.020)

Note: values in ( ) are standard deviations.

Phenology change: The fruit of *R. suavis* became mature earlier in Plot 1 than in Plot 2. The percentage of mature fruits of *R. suavis* in Plot 1 was 92% on July 12, but it was only 52% in Plot 2. The average single fruit weight of *R. suavis* was 0.578 g in Plot 1 and 0.542 g in Plot 2, but they were not statistically significant (P=0.1092>0.05).

DISCUSSION

In this research we only chose one plot for water limitation treatment, because of the difficulty to cover the plot during rains and it includes sufficient replications of the common species in this forest community. Therefore,

we consider that results from one plot under water limitation could be used to explain the response of community and species to environment.

Soil water content change: After the experiment began, water could enter Plot 1 below 1.0 m soil depth by underground runoff, permeation and through the effect of soil capillaries. Plot 1 and Plot 2 cost similar quantity of water from June 24 to July 12. Due to limited water sources to Plot 1, after two weeks, the difference of soil water content distribution at 1.0 m horizon began to appear. The plants in Plot 1 and Pot 2 are very young and their roots mainly are located at less than 50 cm of soil surface. Therefore, at Plot 1 the soil water content mainly decreased from soil surface to 40 cm depth. Because of the limited water supply and the plants' water consumption, there were differences in soil water input and uptake on Plot 1 and Plot 2. For Plot 1 soil water input occurred mainly at depth of 30-40 and 80-100 cm, but for Plot 2 soil water was available at the soil surface, 20-40 and 80-100 cm depth. Soil water was consumed mainly at 0-20 and 50-70 cm depth in Plot 1, but it was consumed mainly at 0-30 and 50-80 cm depth in Plot 2.

The spatially heterogeneous distribution of soil water content is the main sources allowing the ecosystem to adapt to water supply limitation or temporary drought pulse. The processes of water input and uptake were changed under drought condition due to water percolation, effects of soil capillaries and difference in plant roots absorbing of soil water. Communities can adapt to drought or water limitation by the spatial and temporal change of soil water uptake and use. Rockström and Rouw[16] and Hodkinson *et al.*[17] indicated that spatial variation of water availability is important to living organisms. In this study, for both plots soil water contents were always higher at soil surface of 0-10 cm and soil moisture changed more rapidly in shallow soil than at deep horizons.

Soil nutrient change: Research on soil nutrient dynamics in natural communities or ecosystems under drought or water limitation is limited. In this study soil P, K and S in Plot 1 and Plot 2 had similar behaviors during the water limitation or temporary drought pulse. Soil C and N dynamics seemed complicated. For Plot 1 soil C content decreased, but it increased in Plot 2. Soil N content increased slightly but decreased at Plot 1 on July 12; however, it continued to increase on Plot 2. Buljovcic and Engels[18] indicated that N-uptake of roots was reduced to about 20% when the soil water content was decreased to 5%, but it recovered after re-watering. Soil drought decreases mineralization of organically bound nutrient

and nutrient transport in soil by mass flow and diffusion[19-21] and thus may decrease nutrient availability at the root surface. Severe drought may further decrease nutrient transport to root surfaces by inducing root shrinkage and thus loss of soil–root contact[22]. Therefore, nutrient uptake may be inhibited by dry soil and it may be expected that soil nutrient concentrations increase under drought condition. In this research only the total K obviously increased in Plot 1. Egilla *et al.*[23] found that adequate K nutrient could improve drought resistance and root longevity in *Hibiscus rosa-sinensis*. But the effect of soil drought on nutrient uptake or root growth may also dependent on the intensity of drought and its spatial distribution. Drought induces increased deposition of hydrophobic substances in the wall of epidermal root cells, so that may reduce the hydraulic conductance of the root and also affect apoplastic nutrient transport and apoplastic accessibility of the membranes for nutrients[24,25]. However, BassiriRad *et al.*[26] argued the conflicting results for the effect of soil drought on nutrient uptake. Substantial drought-induced decrease in uptake ability was found for P in barley[27] and rye grass[28] and for N in *Pseudoroegneria spicata* and *Artemisia tridentate*[29,30]. But soil drought did not affect the uptake ability for N in *Agropyron desertorum*[29] and even increased the uptake ability for P in *Artemisia tridentate*[31]. Matzner and Richards[31] found the uptake ability of *Artemisia tridentate* for N decreased under mild water stress, but was not further decreased by severe water deficit. Because different species had different uptake ability under different soil water content, the soil nutrient dynamics in ecosystems may be quite complicated. In this study soil K continuously increased under soil water limitation or drought. Therefore, soil K may enhance community resistance to drought. The further research of the nutrient uptake in the specific ecosystem should be furthered.

Soil respiration rate: The variability of soil surface respiration has been attributed to species composition, stand age, management practices and climatic and edaphic conditions[32-35]. In this study we found that the soil water conditions can also effect on soil respiration and soil respiration increased significantly as the soil water content decreased. Multiple factors contribute to the differences in soil respiration, generally low soil moisture, high soil temperature and soil organic matter content resulted in high soil respiration. Xu and Qi[36] found that soil moisture affects soil respiration combining with temperature. For measurements where soil moisture was lower than 14%, soil temperature explained about 60% of the variance of soil respiration. When soil moisture was

higher than 14%, soil temperature explained 73% of the variance of CO_2 efflux. They further indicated that summer drought limited soil CO_2. Billings *et al.*[37] argued that soil did not experience apparent moisture stress and the soil respiration mainly followed the temporal variation of the soil temperature. However, soil respiration resulted from microbial activity in the decomposition and roots respiration and about 30-90% was from roots respiration[38-40]. The present research we found that soil respiration was related to soil water content, but the relationship between soil water content of each soil horizon and soil respiration was not significant. The same pattern was found with air temperature because the soil respiration included roots respiration. Joshi[41] showed that increased soil respiration followed an increase in total N, P, organic matter and fine root biomass. Elliot *et al.*[42] indicated the importance of soil pore space for microbial activity and soil CO_2 efflux.

Plant leaf parameter: The lack of adequate soil moisture leads to water deficits in leaf tissue, affecting many physiological processes[43]. In our study water content and water potential of plant leaves were sensitive to change of soil water content. Leaves of main plant species in Plot 1 decreased their water content dramatically; leaf water potentials of main species were lower than the same species in Plot 2. The leaf water content of most species was sensitive to soil water limitation, such as *A. mono, Q. mongolica, T. amurensis, P. davidiana, C. maximowiczii, B. platyphylla, P. polypodioides* and *P. koraiensis*. Iannucci *et al.*[44] indicated that drought acclimation in berseem clover contributed to water stress tolerance by the maintenance of tissue hydration. The change in leaf water content and water potential may arise from change in osmotic volume in cell wall elasticity and in solute content[45]. The decreasing osmotic potential by net solute accumulation (osmotic adjustment) to water stress results in an improved capacity to maintain turgor at lower water potential. The maintenance of turgor above threshold seems essential for many physiological processes, such as cell expansion, photosynthesis, transpiration, stomatal conductance and finally to continuous growth[46].

In this study the leaf stomatal conductance decreased dramatically for all species in both plots, however, leaf transpiration increased. Usually with the decreasing stomatal conductance, leaf transpiration should be decreased. No similar results were reported in other research; increasing transpiration may be beneficial to cool leaves. Photosynthetic rates of main plant species increased, but changed in two ways. Many species decreased photosynthetic rates first and then increased it dramatically. Other species increased their photosynthetic

rates continuously. We do not know the exact mechanism explaining why plant species respond differently under similar conditions. Photosynthesis is controlled by many factors; one of them is biological character of plant species. In this study we found that most shade-intolerant species increased their photosynthetic rates continuously, while most shade-tolerant and middle shade tolerant species decreased their photosynthetic rates first and then increased. This functional convergence is related to the plants' biological characteristics. The differences in photosynthetic acclimation may relate to species' growth and survival, but the exact causes for the differences are unclear. A possible explanation is that photosynthetic plasticity is related to leaf chemical and structural adaptation[47-49]. Rothstein and Zak[50] argued that the greater range of photosynthetic acclimation of *Viola pubescens* was associated with shifts in allocation between Rubisco and chlorophyll, as well as changes in total leaf nitrogen concentration and leaf mass per area. However, the narrow range of acclimation of *Tiarella cordifolia* was associated soley with changes in allocation to Rubisco versus chlorophyll, with no changes in total leaf nitrogen or leaf mass per area.

Plant growth: Serious water stress could effect the survival, growth and yield of plan species[16,44]. In our study most species in Plot 1 had lower photosynthetic rates; their growth rates in height and stem diameter were lower than those in Plot 2. The likely mechanism is that the lower turgor inhibits cell expansion and lower net photosynthetic rates result in decreased mass accumulation. However, some species in Plot 1 had higher average growth rates in height and stem diameter than the same species in Plot 2, such as *A. mono* and *Picea koraiensis*. Species growth rates may not only depend on photosynthesis, but also may be related to competition with other species and their canopy position in community. Harte and Shaw[51] indicated that the dominance of a montane vegetation community shifted under a warm climate experiment using overhead radiators. A long term water limitation or drought pulse might affect the yield and species composition in the ecosystem. That also means that communities can adapt to temporary water limitation or drought pulse by decreasing growth or change species composition. Species' functional divergence would be facilitated adaptation and survival of this community. Elmqvist *et al.*[52] suggested that response diversity of ecosystem could increase ecosystem resilience in relation to disturbance and human-induced environmental change.

Plant phenology: The fruits of *R. suavis* were matured earlier in Plot 1 than in Plot 2, likely due to the water

limitation. We chose *R. suavis* because their fruits turn into red as they become mature. Proper drought or water limitation is favored in some species, at least for *R. suavis* in this study. Therefore, any environmental change will affect the biological processes in ecosystems. The change of phenology of plant species may change community composition over the long term. In our study we did not find statistically significant difference in average fruit weight of *R. suavis* between Plot 1 and Plot 2. Rockström and Rouw[16] found the effect of water shortage on yield and yield components of pearl millet and grain number dropped significantly due to water shortage. Therefore, phenological change of plant species is another way for community to adapt to water limitation or drought.

In summary, the young natural forest community of mixed broadleaved and coniferous Korean pine forest can adapt to temporary water limitation or drought pulse at different scales, such as from leaf scale to community or ecosystem scale. Plant leaves can adapt by decreasing leaf water contents or water potential and changing photosynthetic rates. Functional convergence and divergence both exist in plant response to the environment. Plant species acclimate to such conditions by changing their growth and phenology. At a community level the spatially heterogeneous distribution of soil water availability and uptake and change of soil nutrients are also the results of the community acclimation. However, the study of the adaptation of natural communities or ecosystems near the threshold of water limitation or drought should be furthered; and research on large scale, such as national or global scale[53,54] would be helpful to make strategies to adapt to global climatic change.

ACKNOWLEDGMENT

REFERENCES

1. Hansen, J., D. Johnson and A. Lacis, 1981. Climatic impact of increasing atmospheric carbon dioxide. Science, 213: 957-966.
2. Hulme, M., T. Wigley, T. Jiang, Z. Zhao, F. Wang, Y. Ding, R. Leemans and A. Markham, 1992. Climate change caused by greehouse effect and its effects to China. WWF International, Gland, Switzerland.
3. Wetherald, R.T. and S. Manabe, 1995. The mechanism of summer dryness induced by greenhouse warming. J. Clim., 8: 3096-3108.
4. Houghton, J.T., F.L.G. Meria, B.A. Callander, N. Harris and K. Maskell, 1996. Climate Change 1995: The science of climate change. Contribution of WG1 to the Second Assesment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
5. Watson, R.T., M.C. Zinyowera, R.H. Moss and D.J. Dokken, 1996. Climate Change 1995, Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analysis. IPCC. Cambridge University Press, Cambridge, UK.
6. Zang, J.J., 1992. Climatic change and its effects on the potential productivity of crops. Chin. Meteorol., 18: 3-6.
7. Yan, M., 1994. Climate change in the Da Hinggan Mountains in recent 36 years. In: Zhao, K., Zhang, W., Zhou, Y., Yang, Y. (Eds.), Impact of forest fire on the environment at Da Hinggan Mountains and the strategies. Science Press, Beijing, pp: 143-148.
8. Research Group of China Climate Change Country Study. 2000. China Climate Change Country Study. Tsinghua University Press, Beijing, pp: 74-140.
9. Chen, X., 2002a. Study on the ecological safety of the forest in Northeast China under climate change. Inter. J. Sustain Dev. World Ecol., 9: 49-58.
10. Chen, X., 2002b. Modeling the effects of global climatic change at the ecotone of boreal larch forest and temperate forest in Northeast China. Clim. Change, 55: 77-97.
11. Chen, X., 2002c. Change of water vapor exchange properties of 3 tree species under drought. J. Arid Environ., 51: 423-435.
12. Meinzer, F.C., 2003. Functional convergence in plant responses to the environment. Oecologia, 134: 1-11.
13. Odum, E.P., 1981. The effects of stress on the trajectory of ecological succession. In: Barrett, G.W., Rosenberg, R. (Eds.), Stress Effects on Natural Ecosystems. John Wiley and Sons, New York, pp: 43-47.
14. Yang, H., Z. Wang, J.N.R. Jeffers and P.A. Ward, 1987. The Temperate Forest Ecosystem. Institute of Terrestrial Ecology, Merlewood Research Station, Grange-over-Sands, Cumbria, LA11 6JU, pp: 7.
15. Turner, N.C., 1981. Techniques and experimental approaches for the measurement of plant water status. Plant Soil, 58: 339-366.
16. Rockström, J. and A. de Rouw, 1997. Water, nutrients and slope position in on-farm pearl millet cultivation in the Sahel. Plant Soil, 195: 311-327.

17. Hodkinson, I.D., N.R. Webb, J.S. Bale and W.Block, 1999. Hydrology, water availability and tundra ecosystem function in a changing climate: the need for a closer integration of ideas? Global Change Bio., 5: 359-369.

18. Buljovcic, Z. and C. Engels, 2001. Nitrate uptake ability by maize roots during and after drought stress. Plant Soil, 229: 125-135.

19. Bloem, J., P.C. De Ruiter, G.J. Koopman, G. Lebbink and L. Brussaard, 1992. Microbial numbers and activity in dried and rewetted arable soil under integrated and conventional management. Soil Biol. Biochem., 24: 655-665.

20. Walwortth, J.L., 1992. Soil drying and rewetting, or freezing and thawing, affects soil solution composition. Soil Sci. Soc. Am. J., 56: 433-437.

21. Seiffert, S., J. Kaselowsky, A. Jungk and N. Claassen, 1995. Observed and calculated potassium uptake by maize as affected by soil water content and bulk density. Agro. J., 87: 1070-1077.

22. North, G.B and P.S. Nobel, 1997. Root-soil contact for the desert succulent *Agave deserti* in wet and drying soil. New Phytol., 101: 1305-1315.

23. Egilla, J.N., F.T.Jr. Davies and M.C. Drew, 2001. Effect of potassium on drought resistance of *Hibiscusrosa-sinensis* cv. Leprechaun: Plant growth, leaf macro- and micronutrient content and root longevity. Plant Soil, 229: 213-224.

24. Ferguson, I.B. and D.T. Clarkson, 1976. Ion uptake in relation to the development of a root hypodermis. New Phytol., 77: 11-14.

25. Peterson, C.A., 1987. The exodermal casparian band of onion roots blocks the apoplastic movement of sulphate ions. J. Exp. Bot., 38: 2068-2081.

26. BassiriRad, H., D.C. Tremmel, R.A. Virginia, J.F. Reynolds, A.G. de Soyza and M.H. Brunell, 1999. Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. Plant Ecol., 145: 27-36.

27. Shone, M.G. and A.V. Flood, 1983. Effects of periods of localized water stress on subsequent nutrient uptake by bareley roots and their adaptation by osmotic adjustment. New Phytol., 94: 561-572.

28. Jupp, A.P. and E.I. Newman, 1987. Phosphorus uptake from soil by *Lolium perenne* during and after drought. J. Appl. Ecol., 24: 979-990.

29. BassiriRad, H. and M.M. Caldwell, 1992a. Root growth, osmotic adjustment and NO uptake during and after a period of drought in *Artemisia tridentata*. Austral J. Plant Physiol., 19: 493-500.

30. BassiriRad, H. and M.M. Caldwell, 1992b. Temporal changes in root growth and ^{15}N-uptake and water relations of two tussock grass species recovering from water stress. Physiol. Plantum, 86: 525-531.

31. Matzner, S.T. and J.H. Richards, 1996. Sagebrush (*Artemisia tridentate* Nutt.) roots maintain nutrient uptake capacity under water stress. J. Exp. Bot., 47: 1045-1056.

32. Edwards, N.T. and B.M. Ross-Todd, 1983. Soil carbon dynamics in a mixed deciduous forest following clear-cutting with and without residue removal. Soil Sci. Soc. Am. J., 47: 1014-1021.

33. Ewel, K.C., W.P. Cropper and H.L. Gholz, 1987. Soil CO_2 evolution in Florida slash pine plantations. I. Changing through time. Can. J. For. Res., 17: 325-329.

34. Toland, D.E. and D.R. Zak, 1994. Seasonal patterns of soil respiration in intact and clear-cut northern hardwood forests. Can. J. For. Res., 24: 1711-1716.

35. Nakane, K. and N.J. Lee, 1995. Simulation of soil carbon cycling and carbon balance following clear-cutting in a mid-temperate forest and contribution to the sink of atmosphere. Vegetatio, 121: 147-156.

36. Xu, M. and Y. Qi, 2001. Soil-surface CO2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. Global Change Bio., 7: 667-677.

37. Billings, S.A., D.D. Richter and J. Yarie, 1998. Soil carbon dioxide fluxes and profile concentrations in two boreal forests. Can. J. For. Res., 28: 1773-1783.

38. Bowden, R.D., K.J. Nadelhoffer, R.D. Boone, J.M. Melillo and J.B. Garrison, 1993. Contributions of aboveground litter, belowground litter and root respiration to total soil respiration in a temperate mixed hardwood forest. Can. J. For. Res., 23: 1402-1407.

39. Thierron, V. and H. Laudelout, 1996. Contribution of root respiration to total CO_2 efflux from the soil of a deciduous forest. Can. J. For. Res., 26: 1142-1148.

40. Epron, D., L. Farque, E. Lucot and P.M. Badot, 1999. Soil CO_2 efflux in a beech forest: the contribution of root respiration. Ann. For. Sci., 56: 289-295.

41. Joshi, M., 1994. Patterns of forest floor respiration in broadleaf and conifer forest ecosystems in parts of central Himalaya. Proc. Indian Nat. Acad. Sci. B, 60: 67-74.

42. Elliot, E.T., R.V. Anderson, D.C. Coleman and C.V. Cole, 1980. Habitat pore space and microbial trophic interactions. Oikos, 35: 327-335.

43. Hsiao, T.C., 1973. Plant response to water stress. Annu. Rev. Plant Physiol., 24: 519-570.

44. Iannucci, A., A. Rascio, M. Russo, N. Di Fonzo and P. Martiniello, 2000. Physiological response to water stress following a conditioning period in berseem clover. Plant Soil, 223: 217-227.

45. Turner, N.C. and M.M. Jones, 1980. Turgor maintenance by osmotic adjustment: A review and evaluation. In: Turner, N.C., Kramer, P.J. (Eds.), Adaptation of Plants to Water and High Temperature Stress. Wiley and Sons, New York, pp: 87-103.

46. Tyree, M.T. and P.G. Javis, 1982. Water in tissues and cells. In: Langes, O.L., Nobel, P.S., Osmond, C.B., Ziegler, M. (Eds.), Encyclopedia of Plant Physiology, New Series, Springer-Verlag, Berlin, 120:36-77.

47. Chabot, B.F. and D.J. Hicks, 1982. The ecology of leaf life spans. Annu. Rev. Ecol. Syst., 13: 229-259.

48. Field, C. and H.A. Mooney, 1986. The photosynthesis nitrogen relationship in wild plants. In: Givnish, T.J. (Ed.), On the Economy of Plant Form and Function. Cambridge University Press, Cambridge, UK, pp: 25-55.

49. Reich, P.B., M.B. Walters and D.S. Ellsworth, 1992. Leaf life span in relation to leaf, plant and stand characteristics among diverse ecosystems. Ecol. Monogr., 62: 365-392.

50. Rothstein, D.E. and D.R. Zak, 2001. Photosynthetic adaptation and acclimation to exploit seasonal periods of direct irradiance in three temperate, deciduous-forest herbs. Fun. Ecol., 15: 722-731.

51. Harte, J. and R. Shaw, 1995. Shifting dominance within a montane vegetation community: results of a Climate-Warming experiment. Science, 267: 876-880.

52. Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker and J. Norberg, 2003. Response diversity, ecosystem change and resilience. Front. Ecol. Environ., 1: 488-494.

53. Braswell, B.H., D.S. Schimel, E. Linder and B. III. Moore, 1997. The response of global terrestrial ecosystems to interannual temperature variability. Science, 278: 870-872.

54. Behrenfeld, M.J., J.T. Randerson, C.R. McClain, G.C. Feldman, S.O. Los, C.J. Tucker, P.G. Falkowski, C.B. Field, R. Frouin, W.E. Esaias, D.D. Kolber and N.H. Pollack, 2001. Biospheric primary production during an ENSO transition. Science, 291: 2594-2597.

55. Guo, L.B. and R.M. Gifford, 2002. Soil carbon stocks and land use change: a meta analysis. Global Change Bio., 8: 345-360.