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Hill Slope Variations in Chlorophyll Fluorescence Indices and Leaf Traits in a Small Arctic Watershed

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Abstract

Physiological processes responsible for ecosystem carbon and nitrogen cycling may vary across hill slopes and be controlled by watershed hydrology and the associated nutrient transport. Mass transport of nutrients down slope and into water tracks may increase nutrient delivery to plant roots, nutrient uptake, and perhaps photosynthetic activity. Small arctic watersheds are commonly characterized by increased biomass, particularly of woody deciduous shrubs, both down slope and in water tracks. We ask if photosynthetic physiology varies with hill slope position and if it is correlated to observed changes in above ground biomass. Chlorophyll fluorescence surveys from six common species reveal that maximum photosynthetic electron transport decreased significantly (by as much as 85%) down slope in 4 species. Leaf nitrogen concentrations varied from 1 to 2.5% across all leaves sampled, but show little trend with hill slope position, and as a result are not well correlated with photosynthetic electron transport. We hypothesize that trace metal concentrations may have increased in the leaves of plants growing in down slope positions and that this may be responsible for the reduction in electron transport. The relationship between the measured maximum energy conversion by photosystem II and maximum electron transport rate is species specific and indicative of light adaptation in these arctic species. Increased plant growth down slope and in water tracks does not appear to be correlated to the physiological parameters measured and instead are more likely a product of increased canopy nitrogen concentrations and leaf area accumulation.

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Introduction

It is well recognized that processes influenced by hill slope position and landscape age determine vegetation distribution in arctic ecosystems (Bliss, 1956; Chapin et al., 1988; Walker et al., 1994). For example, along many hill slope gradients arctic ecosystems transition from a dry heath tundra at the hill top or ridge crest to the ubiquitous tussock tundra community mid-slope and then to a wet sedge community near the valley bottom (Walker et al., 1989) as resources such as water and nitrogen vary (Rastetter et al., 2004; Yano et al., 2010). Furthermore, since the productivity of arctic ecosystems is known to be strongly nitrogen limited (Chapin et al., 1988; Jonasson et al., 1999; Shaver et al., 2001; Weintraub and Schimel, 2005b), it is logical to predict, and important to quantify, linkages among the biogeochemical processes influencing carbon gain and landscape position. Within a watershed, the movement of both carbon (C) and nitrogen (N) is controlled by a combination of hydrology, biology, chemistry, and the physical drivers of climate, all of which can vary along a hill slope. For this reason it is important to know how plant physiological activity varies along a hill slope and among different species and/or functional types.

Previous research in the arctic tundra has shown that variability in species abundance across the landscape is more strongly related to different levels of nitrogen and phosphorous than to water availability, length of snow-free season, or soil pH (Miller, 1982), and this clearly has important implications for hill slopes. Furthermore, it has been shown that the absorption of nutrients in arctic tundra is primarily controlled by the rate of nutrient supply to the root surface, rather than by plant physiological characteristics

(Chapin et al., 1988; Schimel et al., 1996; Weintraub and Schimel, 2005a), again linking this problem to hill slope hydrology, which can control the availability of soluble nutrients down slope. While water availability itself may not directly determine species variability, the extent of water flow in arctic watersheds can substantially modify N and P cycling and thus plant community structure. Increased mass flow alleviates the limitations of nutrient uptake imposed by ion diffusion (Chapin et al., 1988) and should enhance nutrient availability down slope and therefore stimulate productivity.

The Innvait Creek watershed, in the Low Arctic of Alaska, north of the Brooks Range, has proven to be a valuable site for the study of hill slope hydrology (Kane et al., 1989, 1990, 2000; McNamara et al., 1999; Stieglitz et al., 1999, 2000, 2003), biogeochemistry (Kay and Virginia, 1989; Moorhead and Reynolds, 1993; Gebauer et al., 1996; Leadley et al., 1997; Cheng et al., 1998; Hobara et al., 2006), and plant physiological processes (Oberbauer et al., 1989, 1991; Leadley et al., 1997; Gebauer et al., 1998; Hobara et al., 2006). Particular features of interest are hill slope water tracks, which are shallow drainage channels spaced tens of meters apart and are common on the mid- to lower portions of most hills (McNamara et al., 1999). Water tracks increase mass flow through tussock tundra and are areas where deciduous shrub species have become dominant (Walker et al., 1994; Gebauer et al., 1996). In fact, while some water tracks can be identified by distinct channels, many others are more subtle and can only be discerned by a greater abundance of dwarf willows (*Salix pulchra*), dwarf birch (*Betula nana*), and cloud berry (*Rubus chamaemorus*), relative to adjacent tundra (Walker et al., 1994). It has been suggested that root strate-

gies unique to the deciduous species found at Imnavait Creek may allow them to more easily capture nutrients from the soil and thus to capitalize on a greater nutrient influx (Schimel et al., 1996). What is not known, however, is if water track plants are able to capitalize on the nearly continuous root exposure to a dilute nutrient solution (Chapin et al., 1988) by altering leaf-level physiology. Fertilization experiments in the Imnavait Creek watershed demonstrate that leaves from water track plants located downslope of nutrient additions can respond with higher nutrient concentrations and increased photosynthetic rates (Oberbauer et al., 1989), but a later study of landscape patterns of leaf photosynthesis found a more complicated species-dependent pattern and generally decreasing photosynthetic rates down slope (Oberbauer et al., 1996). With only these few tundra specific studies having been published, the quantification of hill slope variation in physiological factors related to plant carbon balance remains an important but insufficiently answered question.

Here we examine variability in plant physiological activity along a hill slope as a means to assess some of the key relationships between the critical drivers and processes influencing plant and ecosystem form and function. We employed a chlorophyll fluorescence method to examine the photosynthetic activity of species along a hill slope in the Imnavait Creek watershed, to address our initial hypothesis: that increased photosynthetic electron transport would be found in areas of high relative water and thus high nutrient influx; and that this photosynthetic increase would be most pronounced in the deciduous shrub species that dominate areas of high moisture in tussock tundra (i.e. in water tracks). Many C_3 species show large increases in photosynthesis with increased leaf N concentrations (Field and Mooney, 1986), thus leading us to specifically predict that photosynthetic electron transport will increase both down slope and within the hill slope water tracks due to the accumulation of resources through mass flow and ecosystem hydrology (Chapin et al., 1988). We strive for a better understanding of the spatial distribution of physiological activity on the hill slope and ultimately of the integrated biogeochemical cycles of the watershed.

Materials and Methods

SITE

The Imnavait Creek watershed is a small 2.2 km² catchment located near the Toolik Lake Field Station (location of the arctic LTER) in the northern foothills of the Brooks Range, about 250 km south of Prudhoe Bay, Alaska, U.S.A. (68°37'N, 149°18'W). Elevation ranges between about 960 and 840 m a.s.l. (McNamara et al., 1998), with gently rolling hills rising less than 100 m from the beaded stream in the valley. Since the mid-1980s, the climate, hydrology, and energy balance of Imnavait Creek have been studied continuously (Hinzman et al., 1996, 1998; Schramm et al., 2007). Multiyear records of soil thaw, precipitation, and stream flow exist (Everett et al., 1996; Nelson et al., 1998), and a weather station with rare winter snowfall records has operated year-round since 1975 (SNOTEL site 968, <http://www.wcc.nrcs.usda.gov/snotel>). Mean annual temperature is typically between -7 and -8 °C, and mean annual precipitation is about 35 cm (Reynolds and Tenhunen, 1996; Yano et al., 2010). The watershed includes heath vegetation at ridge crest locations and wet sedge vegetation in riparian areas,

with the majority of the watershed being dominated by tussock tundra vegetation. A detailed discussion of the terrain and vegetation of the Imnavait Creek watershed can be found in Walker and Walker (1996).

This study specifically seeks to examine the distribution of physiological activity on the hill slope and secondary factors that allow deciduous shrub species to significantly increase their dominance in water tracks, as opposed to the adjacent areas where they are present, but not necessarily prevailing. For this purpose, a well-defined water track on the west-facing slope of Imnavait Creek watershed was chosen for intensive study during the peak of the growing season when physiological activity is known to be its highest (all field measurements reported here were made from late June to mid-July 2003). Eight sample locations running from the ridge crest to the beaded stream, each 100 m apart, were used (Table 1). The elevation change along the 800-m-long sampling transect, from ridge crest to beaded stream, is 52 m. At each location, sampling occurred both in the water track (WT) and in the adjacent non-water track (NWT) for a total of 16 sample sites (WT and NWT at each of 8 hill slope locations). Our measurements were made in conjunction with a much larger modeling project linking hill slope hydrology and biogeochemistry and thus the paired WT vs. NWT locations were chosen for consistency with the instrumented water tracks. Six different species were used: two woody deciduous shrubs (*Betula nana* L. and *Salix pulchra* Cham.), two perennial herbs (*Rubus chamaemorus* L. and *Petasites frigidus* L.), and two ericaceous evergreen shrubs (*Vaccinium vitis-idaea* L., and *Ledum palustre* L.). It should be noted that many researchers classify *R. chamaemorus* as a deciduous shrub; however due to the lack of a perennial above ground stem, we have chosen to classify this species as a perennial herb (Viereck and Little, 2007). Our species choices purposely incorporated many of the major vegetative types and microenvironments present in the watershed, while allowing a species to be sampled at every site in a single day to avoid complications due to rapidly changing environmental conditions.

CHLOROPHYLL FLUORESCENCE

A field portable chlorophyll fluorometer (FMS II, Hansatech Instruments Limited, Norfolk, U.K.) was used to measure the *in situ* electron transport rate (ETR) during rapid light curves (RLC), as in White and Critchley (1999). ETR is calculated as:

$$ETR = \Phi_{II} \times 0.42 \times PAR, \quad (1)$$

where Φ_{II} is the photochemical quantum yield of PSII as in Genty et al. (1989), PAR is the photosynthetically active radiation (photons of 400 and 700 nm)—making the assumption that an average leaf absorbs 84% of the incident PAR, and accounting for the fact that transport of a single electron requires the absorption of two quanta. The maximum rate of electron transport (ETR_{max}), was determined from the point of light saturation of a plot of ETR against the ambient PAR, and is species dependent. Each RLC consisted of the fluorescence responses to 10 increasing actinic irradiances of 15 s duration, and separated by a 0.8 s saturating flash from a white halogen lamp. Each leaf was dark adapted for a minimum of 20 min prior to sampling. ETR_{max} was measured on a single, fully developed, visually healthy, and free-from-mites

TABLE 1

Physical description of the eight sample locations both within (WT) and between (NWT) the water tracks in the Imnavait creek watershed. Less than 20 m separated the WT and NWT sites, and these sites were at similar hill slope positions. Sample locations were numbered from the top of the hill slope (location 1) to the beaded stream (location 8). Soil moistures are given as percent of capacity of volumetric water content. Thaw Depth was measured on 4 July to the nearest cm and soil moisture (θ) was recorded on 8 July 2003 (WT/NWT comparison). The difference within a specific location is presented as the % change from the NWT to the WT.

	Hill Slope Position							
	1	2	3	4	5	6	7	8
<i>UTM Coordinates (easting)</i>	406600	406500	406400	406300	406200	406100	406000	405900
<i>(northing)</i>	7612600	7612600	7612600	7612600	7612600	7612600	7612600	7612600
<i>Elevation (m)</i>	939	932	921	909	898	890	887	887
<i>θ – WT (%)</i>	28	28	50	75	89	88	91	97
<i>θ – NWT (%)</i>	24	31	48	55	62	71	87	98
<i>$\Delta \theta$ (%)</i>	16.7	–9.7	4.2	36.4	43.5	23.9	4.6	–1.0
<i>Thaw Depth WT (cm)</i>	21	24	22	19	26	21	30	30
<i>Thaw Depth NWT (cm)</i>	20	21	22	20	15	17	24	29
<i>Δ Thaw Depth (%)</i>	5.0	14.3	0.0	–5.0	73.3	23.5	25.0	3.4

or fungi, full sun leaf from three randomly chosen replicate plants per species at each of the 16 sampling locations. For the evergreen species, these leaves were consistently the youngest fully developed leaves present. Typically all measurements on a single species were completed within a 2 to 3 h time period and began between 8:00 a.m. and 3:00 p.m. mean local time, on sunny days only, with one or two species measured per day. The initial hill slope sampling point was varied randomly but ran either from the top to the bottom, or from the bottom to the top of the transect. Importantly, sunlight was continuous during this time of year. The first point of the RLC represented the dark-adapted F_v/F_m , a parameter related to the efficiency of PSII electron transport.

SPECTRAL REFLECTANCE DATA

Spectral reflectance measurements were made at the canopy scale with a field portable spectrometer (Unispec, PP Systems, Haverhill, Massachusetts, U.S.A.) equipped with fiber optics with a 20° field of view, as in Boelman et al. (2003). Hyper-spectral data (300–1100 nm, in 256 different bands) were used to calculate the normalized-difference vegetation index (NDVI; Rouse et al., 1974), and the water band index (WBI; Peñuelas et al., 1993). Specifically:

$$\text{NDVI} = (R_{800} - R_{660}) / (R_{800} + R_{660}), \quad (2)$$

$$\text{WBI} = R_{900} / R_{970}, \quad (3)$$

where R_x is reflectance at the indicated wavelength (nm). Five replicate reflectance spectra were taken over a square meter centered at each sampling spot. Canopy leaf area index (LAI) was estimated from NDVI using the relationship described by Shaver et al. (2007) that was derived from measurements made in this watershed:

$$\text{LAI} = 0.0026e^{8.0783\text{NDVI}}. \quad (4)$$

PLANT AND SITE CHARACTERISTICS

A minimum of 10 leaves from at least 5 different individual plants for each species at each location were collected and dried

for a minimum of 48 h in a 60 °C oven. Dried leaf material from each of the 6 species studied was ground to fine powder for nitrogen analysis with a CHNS/O analyzer (2400 Series II, Perkin-Elmer, Boston, Massachusetts, U.S.A.). Soil-thaw depth measures were taken using a simple depth probe that was thrust into the ground in triplicate on each of the following dates in July 2003: 3, 8, 11, 13, 15, and 17. Additional soil moisture measurements were taken with a handheld time-domain-reflectometry (TDR) probe (Hydrosense, Campbell Scientific, Logan, Utah, U.S.A.) calibrated for these soils. Soil moisture measurements were taken in triplicate and are reported as percent capacity of volumetric water content.

DATA ANALYSIS

Statistical analysis was performed using Data Desk (version 6.2.1, Data Description, Ithaca, New York, U.S.A.). We tested the effect of hill slope position and WT vs. NWT on leaf C and N concentrations and chlorophyll fluorescence values using analysis of variance (ANOVA), followed by multiple comparisons using a least significant difference (LSD) test, assuming a significance level of $P < 0.05$.

Results

The eastern ridge of the Imnavait Creek watershed was relatively dry, with less than 30% soil moisture at the first 2 sampling locations (Table 1). Soil moisture increased significantly down slope, becoming nearly saturated near the beaded stream in the valley bottom. The WT sites became visually distinguished from the adjacent NWT sites at sample locations 4, 5, and 6 where there is, respectively, 36%, 44%, and 24% higher soil moisture availability in the WT. By location 7, the entire slope was wet, and the WT was again less clearly defined. At location 8 in the riparian area, the WT had nearly disappeared, and the vegetation had shifted from tussock tundra to a wet sedge community. Thaw depths varied from 19 to 30 cm with the deepest thaw at the bottom of the hill slope (location 8; Table 1). At low hill slope positions (locations 5, 6, and 7) thaw depths tended to be higher (73, 24, and 25%) in the WT compared to the NWT.

TABLE 2

Leaf area index and water band index from spectral reflectance of the eight sample locations both within (WT) and between (NWT) the water tracks in the Imnavait creek watershed. Hyperspectral information was recorded from three plots at each sample location and used to derive the mean and standard error of the leaf area index (LAI from NDVI) and the water band index (WBI) at each sample location. The difference within a specific location is presented as the % change from the NWT to the WT.

	Sample Location							
	1	2	3	4	5	6	7	8
LAI_{WT}	0.47 ± 0.004	0.47 ± 0.004	0.51 ± 0.003	0.43 ± 0.003	1.1 ± 0.003	1.67 ± 0.003	0.7 ± 0.003	0.3 ± 0.003
LAI_{NWT}	0.28 ± 0.004	0.19 ± 0.004	0.39 ± 0.003	0.34 ± 0.004	0.37 ± 0.003	0.53 ± 0.003	0.42 ± 0.003	0.19 ± 0.003
ΔLAI	0.19	0.28	0.12	0.09	0.73	1.14	0.28	0.11
WBI_{WT}	0.82 ± 0.031	0.98 ± 0.033	0.95 ± 0.028	1.08 ± 0.104	0.91 ± 0.035	1.013 ± 0.02	0.96 ± 0.018	0.97 ± 0.011
WBI_{NWT}	0.91 ± 0.043	1.04 ± 0.070	0.94 ± 0.005	0.86 ± 0.036	0.81 ± 0.038	0.96 ± 0.045	0.99 ± 0.025	0.92 ± 0.020
ΔWBI	-0.09	-0.06	0.01	0.22	0.10	0.06	-0.03	0.05

The increased soil moisture was not correlated with canopy water content as assessed remotely from the WBI (Table 2), but there was a weak positive correlation between thaw depth and WBI (explaining 17 and 35% of the variation in soil moisture in the WT and NWT, respectively).

The canopy leaf area index was maximized at location 6 in both the WT ($LAI = 1.67 \pm 0.003$) and NWT (0.53 ± 0.003 ; Table 2). The difference between the WT and NWT LAI values was maintained over the entire hill slope transect, with a minimum difference at location 4 and a maximum difference at location 6. There was no discernable trend in WT LAI with hill slope position and no relationship between LAI and soil moisture, thaw depth, or WBI.

Leaf C and N concentrations and C:N averaged $50.0\% \pm 0.34$, $1.8\% \pm 0.03$, and 30.8 ± 0.65 , respectively. These values were not significantly affected by the presence of water tracks and thus combined WT and NWT means at each hill slope position are presented in Figure 1. Leaf N in *Vaccinium* was significantly lower than the site mean ($p < 0.05$), averaging $1.02\% \pm 0.004$, and the C:N was significantly higher than the mean of the other five species (51.4 ± 1.9 vs. 25.9 ± 0.92 ; Fig. 1). The highest leaf N was found in *Petasites* at location 6 ($2.76\% \pm 0.2$), and the lowest leaf N was detected in *Vaccinium* at location 8 ($0.86\% \pm 0.1$). There was a weak increasing trend in leaf N concentration down slope in *Betula*, *Petasites*, and *Salix*.

In 4 of the 6 species studied (*Betula*, *Ledum*, *Rubus*, and *Vaccinium*), the dark-adapted ratio of variable to maximum fluorescence (F_v/F_m) was unchanged down slope and did not differ between the WT and NWT locations (Fig. 2). At all locations these four species had F_v/F_m values near 0.8. In *Salix*, F_v/F_m was significantly lower and varied with hill slope position, although this relationship was not monotonic (Fig. 2). The efficiency of energy conversion in *Salix* was low at the ridge crest (dark adapted $F_v/F_m = 0.51 \pm 0.03$ in the WT and 0.54 ± 0.04 in the NWT). *Petasites* also had low dark-adapted F_v/F_m ratios near the top of the slope (0.6 in the WT location 1 and 0.55 at the NWT location 2), and showed a significant trend ($p = 0.03$) of increasing F_v/F_m down slope (reaching 0.74 at WT5 and 0.77 at NWT4, increasing by 40%, respectively).

Rapid light response curves showed species-specific changes in maximum electron transport rate achieved at light saturation

(ETR_{max}) with hill slope position (Fig. 3). The general pattern was a decrease down slope for *Betula*, *Rubus*, *Salix*, and *Vaccinium*, with little difference between WT and NWT locations. The exceptions to this generalization are *Salix* at locations 5 and 7 and *Vaccinium* at location 1, where ETR_{max} was lower in the NWT compared to WT sites. In *Ledum*, ETR_{max} increased from location 1 to location 4 and then decreased again down slope (Fig. 3). *Petasites* again showed a different pattern with an often-significant difference between the WT and NWT sites, with ETR_{max} being lower in the NWT compared to WT sites, except at location 5 (the last location where this species was found), where ETR_{max} was significantly higher in the NWT (Fig. 3). Leaf N was not a strong predictor of either fluorescence parameter (Fig. 4). The PAR level that elicited ETR_{max} was variable, from a low of less than $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *Rubus* to more than $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *Vaccinium* (Fig. 5).

A plot of the efficiency of energy conversion within PSII (dark adapted F_v/F_m) vs. ETR_{max} for each of the species revealed a common intersection for all 6 species, at $F_v/F_m = 0.87$ (excluding *Vaccinium*). Each individual regression line, while significant, explained only a small fraction of the variation in some instances ($R^2 = 0.1$ to 0.8). Regressing the ETR_{max} against the difference between this point of intersection (0.87) and the observed F_v/F_m , separated the six species studied into distinct responses with *Salix* having the smallest slope and *Ledum* the largest (Fig. 6). *Vaccinium* is also displayed in Figure 6 but should be interpreted with extreme caution as the individual regression between dark-adapted F_v/F_m and ETR_{max} for this species was neither statistically significant nor did it pass through the 0.87 common intercept of the other 5 species.

Discussion

Maximum PSII electron transport rates decreased significantly down slope (by as much as 85%) in 4 of the 6 species studied, indicating a strongly reduced rate of excitation energy conversion to electron transport in the photosynthetic apparatus of leaves. This reduction in the activity of the light reactions of photosynthesis was opposite to our prediction of increased activity down slope due to nutrient accumulation yet consistent with Oberbauer et al. (1996). Average leaf nitrogen remained nearly constant down slope, suggesting that the primary response to increased nitrogen availability is at the canopy level, with increased total leaf area,

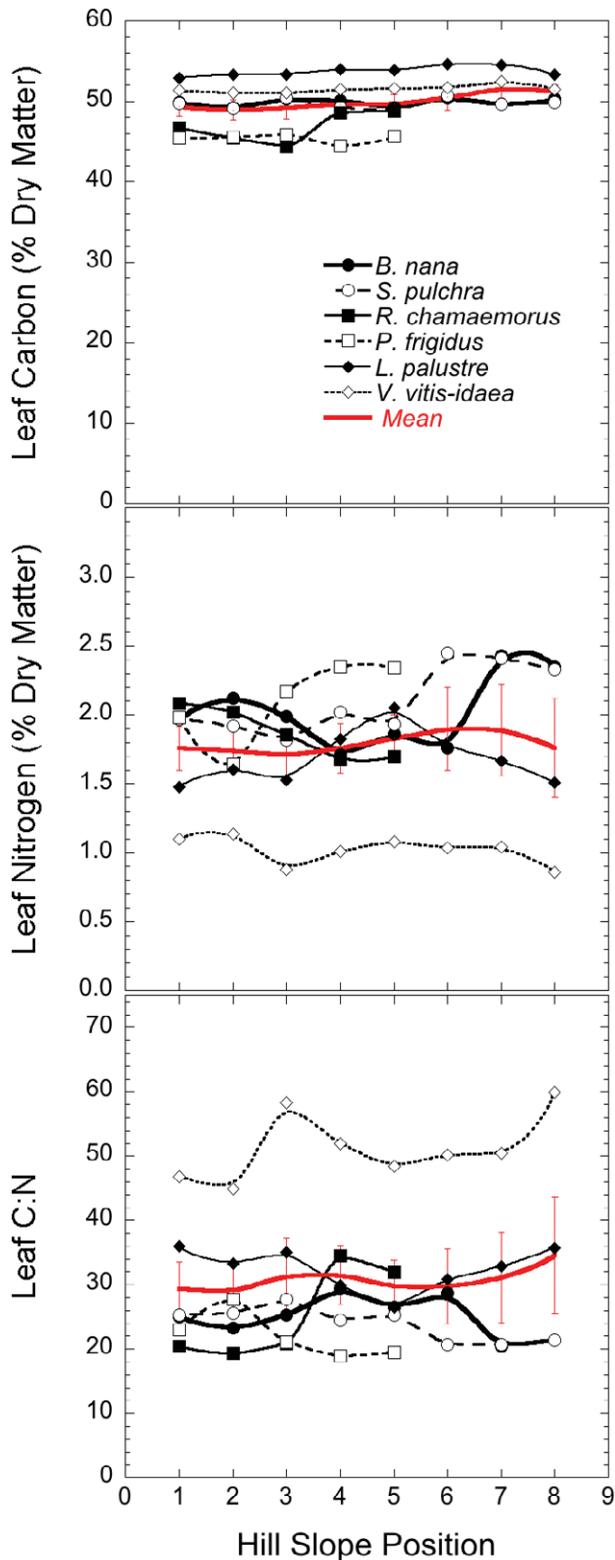


FIGURE 1. Leaf traits as a function of hill slope position (1 is the ridgeline, 8 near the stream bed) in the Imnavait Creek Watershed. Each point is a bulk sample of many leaves from many plants collected from both the WT and NWT locations at the time of the fluorescence measurements and thus represents a mean leaf carbon as a % of the total leaf dry mass (upper) nitrogen as a % of the total leaf dry mass (middle), and carbon to nitrogen ratio (lower) for each species at each site. The site mean (average of all 6 species) is displayed in red and is subtended by the standard error of the mean.

rather than an increased nutrient concentration of individual leaves. In fact, previous research near our field site (Williams and Rastetter, 1999) has demonstrated a nearly constant relationship between leaf area index (LAI) and total foliar nitrogen (N; g m² ground area). In our study, leaf area index reached a maximum at 600 m down slope (location 6), with a value of 1.67 in the WT and 0.53 in the NWT (a 3.5 and 1.9 times increase from the ridge LAI in the two sites, respectively), suggesting an increase in total canopy N accumulation. As a consequence the observed decrease in maximum photosynthetic electron transport was not explained by leaf nitrogen concentration nor was it consistent with the accumulation of above ground biomass. Instead, we suggest other environmental gradients must be responsible.

Water availability did increase down slope increasing from 24–28% saturation at the ridge top to near 100% saturation near the stream, where there was often standing water. The WT locations on the mid- to lower hill slope (positions 4, 5, and 6) tended to have considerably more water (higher % saturation) than the NWT locations, but, regardless, canopy water content changed very little either down slope or between the WT and NWT locations as indicated by the WBI calculated from canopy reflectance. Previous work at Imnavait Creek (Oberbauer et al., 1989) and at the nearby Toolik Lake LTER site (Gebauer et al., 1995, 1998) concluded that water availability rarely limits leaf gas-exchange rates in this ecosystem since tussock tundra vegetation seldom decreases stomatal conductance, even in response to observed humidity deficits. Instead, irrigation experiments have shown that increases in growth resulted from nutrients supplied *via* the water, and not from improved water status itself (Oberbauer et al., 1989, 1996; Oberbauer and Oechel, 1989).

It is possible that the saturated soils were limiting photosynthetic electron transport down slope, but it is curious that so few differences in ETR_{max} were observed between the relatively drier WT and NWT locations and that these differences were opposite to the down slope trends (e.g. higher ETR_{max} in the WT than in the NWT for *Salix* at locations 5 and 7, or *Ledum* at location 4). Thaw depth also increased down slope and in the WT compared to NWT (particularly at positions 5, 6, and 7), and this theoretically could have led to greater decomposition and the possibility of oxygen depletion that could limit photosynthetic performance (Regehr et al., 1975; Gebauer et al., 1995; Dagg and Lafleur, 2011). Yet Oberbauer et al. (1996) reported higher soil CO₂ efflux (which requires sufficient oxygen; Oechel and Billings, 1992) both down slope and in WT compared to NWT locations. The nearly constant flow of water from the Imnavait Creek watershed may keep the soils aerobic.

Another possibility is that these species are adapting to variations in the ambient light environment at the specific microenvironments found either down slope or in the WT locations. Increased LAI certainly results in increased canopy complexity and the potential for a reduced light environment, as do physical differences associated with hummocks and topography. The contrasting response of the two small evergreen plants (*Ledum* and *Vaccinium*), which might be predicted to have the strongest variation in light availability, provide only limited support of such responses, and the very strong decrease in *Betula*, the tallest and most fully sun exposed plant at all locations, also indicates other factors are responsible for the observed changes in fluorescence.

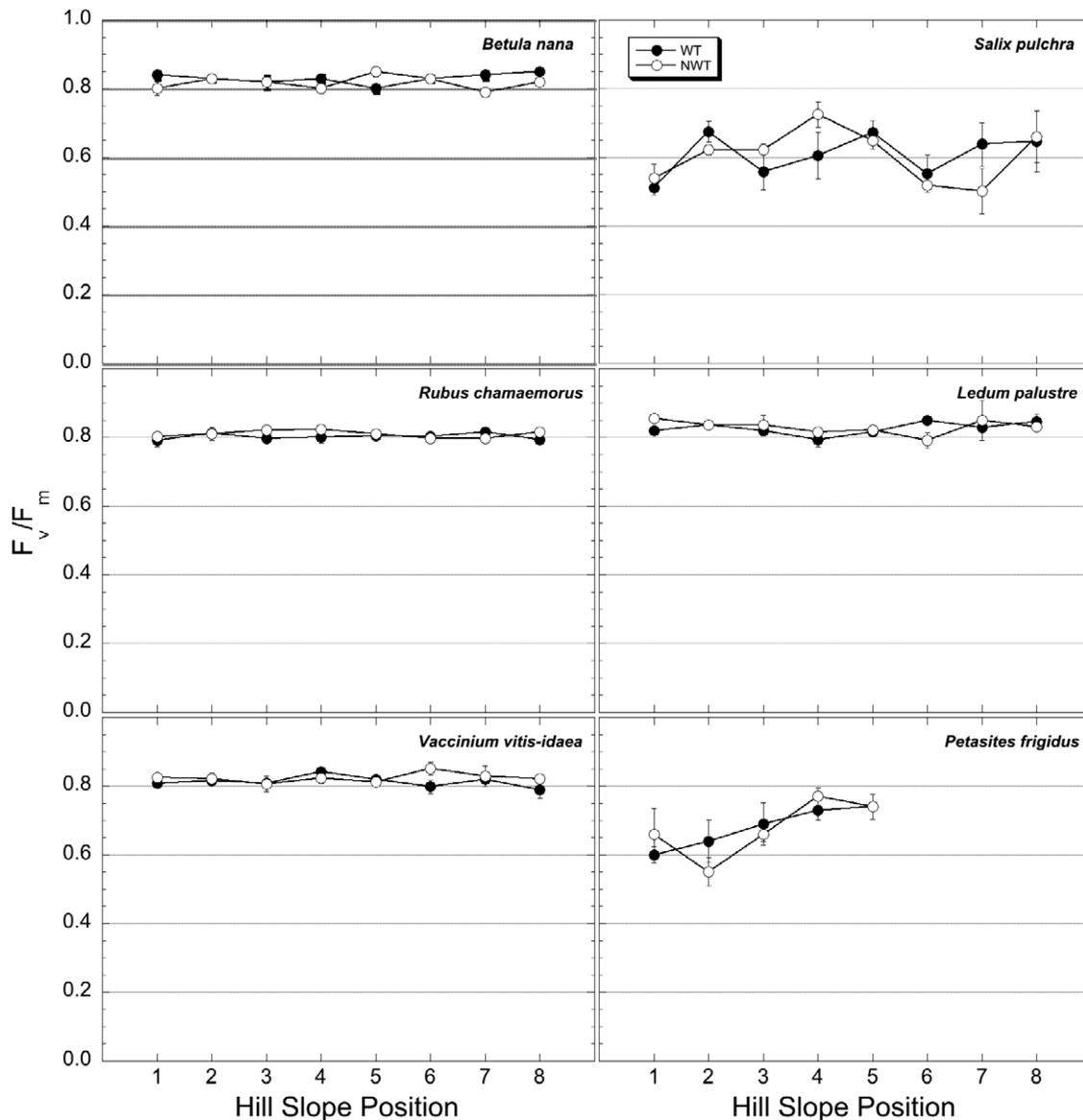


FIGURE 2. Efficiency of energy transfer within the PSII reaction centers of the electron transport system (F_v/F_m —variable to maximum fluorescence) as a function of hill slope position (1 is the ridgeline, 8 near the stream bed) in the Innavaik Creek Watershed. Closed symbols are from within the water tracks, and the open symbols are from the non-water tracks. Each point is the mean of three dark adapted measurements on different leaves at each location and is subtended by the standard error of the mean.

Topographic variation in snowmelt could also potentially affect the phenological development of plants along these hill slope transects (reviewed in Wipf and Rixen, 2010), and the rate of development of several of the species we studied are known to respond to air temperature and or growing degree days (Pop et al., 2000; Wipf, 2010). The initiation of bud break, the completion of leaf expansion, and reproductive activity have all been examined in relation to arctic plant growth and productivity (e.g. Natali et al., 2012) and photosynthetic physiology (e.g. Starr et al., 2000). Unfortunately, we do not have the early season temperature data to test this hypothesis, but found little hill slope variation in air temperature during our measurements. Furthermore, one study from Norway, which included *Betula nana* and *Vaccinium* sp. (two of our most responsive groups), concluded that growth form significantly affects phenology but that topography (slope position and aspect)

does not (Iversen et al., 2009). In light of our observation of strong decreases in maximum electron transport activity down slope, the potential role of phenology deserves more attention and careful study.

Previous work at this location has shown that micronutrients, particularly manganese, can accumulate down slope and can reach potentially toxic levels (Marion et al., 1989). While no visible signs of foliar Mn toxicity were reported by these authors, they communicated that the concentration of this trace metal was found to double in the sediments, from 350 mg kg^{-1} at the ridge of the watershed to 700 mg kg^{-1} in the wet sedge community near the beaded stream. Furthermore, there was a strong vertical distribution of Mn within the soil profile, and the concentration was found to exceed 4000 mg kg^{-1} in the wet Oe horizons where plant roots are typically found (Marion et al., 1989). We suggest this may be the main

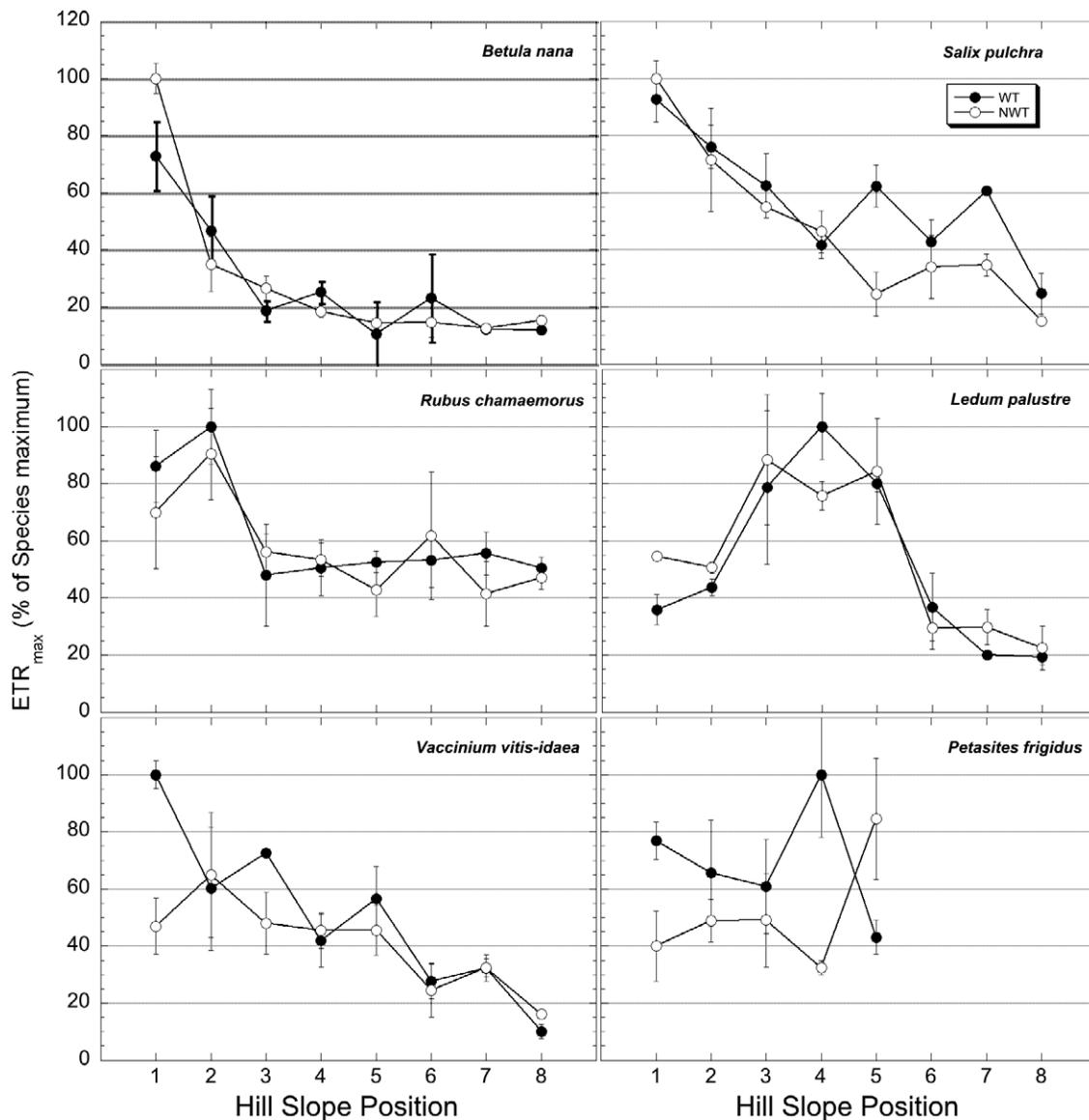


FIGURE 3. Relative maximum PSII electron transport rate (ETR_{max} , $\mu\text{mol electrons m}^{-2}$ leaf area s^{-1}) as a function of hill slope position (1 is the ridgeline, 8 near the stream bed) in the Imnavait Creek Watershed. To emphasize the effect of hill slope position, each point is normalized to the maximum rate of electron transport recorded for that species (*Betula nana*, 39.0 ± 2.6 ; *Salix pulchra*, 25.0 ± 1.6 ; *Rubus chamaemorus*, 11.0 ± 9.9 ; *Petasites frigidus*, 38.9 ± 8.5 ; *Ledum palustre*, 25.9 ± 3.0 ; *Vaccinium vitis-idaea*, 86.3 ± 4.2). Closed symbols are from within the water tracks, and the open symbols are from the non-water tracks. Each point is the mean of three rapid light response curves measured on different leaves at each location and is subtended by the standard error of the mean.

cause of the reduced ETR_{max} observed down slope in 4 of the 6 species surveyed. Chlorophyll fluorescence has been used to assess Mn tolerance in *Betula ermanii* Cham. and three other deciduous tree species native to northern Japan (Kitao et al., 1998). These authors reported that maximum photochemical efficiency of PSII (F_v/F_m) is little affected by a wide range of [Mn] but that the realized yield (ETR_{max}) is reduced by high [Mn]—potentially consistent with our observations at Imnavait creek. The acidic soils and the accumulation of H^+ down slope could increase Mn solubility and accumulation in the colluvial deposits common to the lower foot slope of the watershed (Walker and Walker, 1996).

Two species, *Ledum* and *Petasites*, did not show the same generalized trend of decreasing ETR_{max} down slope, and two species, *Salix* and *Petasites*, had $F_v/F_m < 0.8$, indicating a reduced

PSII efficiency and some level of stress. *Ledum* has been shown to prefer the less mobile nitrogen species NH_4^+ over NO_3^- or amino acid sources and is further distinguished from *Vaccinium* and *Betula* in its N acquisition both temporally, acquiring N early in the growing season (as compared to *Betula*), and spatially, by utilizing N from the entire active layer rather than predominately from the upper 3 cm (McKane et al., 2002). We found a similar pattern in ETR_{max} and leaf [N] in *Ledum*, both peaking mid-slope, and a suggestive positive correlation between Leaf N and ETR_{max} ($p = 0.12$). *Salix* is far less common on the hill slope than *Betula*, the other deciduous shrub commonly found in the watershed, and its reduced F_v/F_m indicates a moderate level of stress (Björkman and Demmig, 1987), which may have been consistent with the low light level required to achieve ETR_{max} in this species and the very

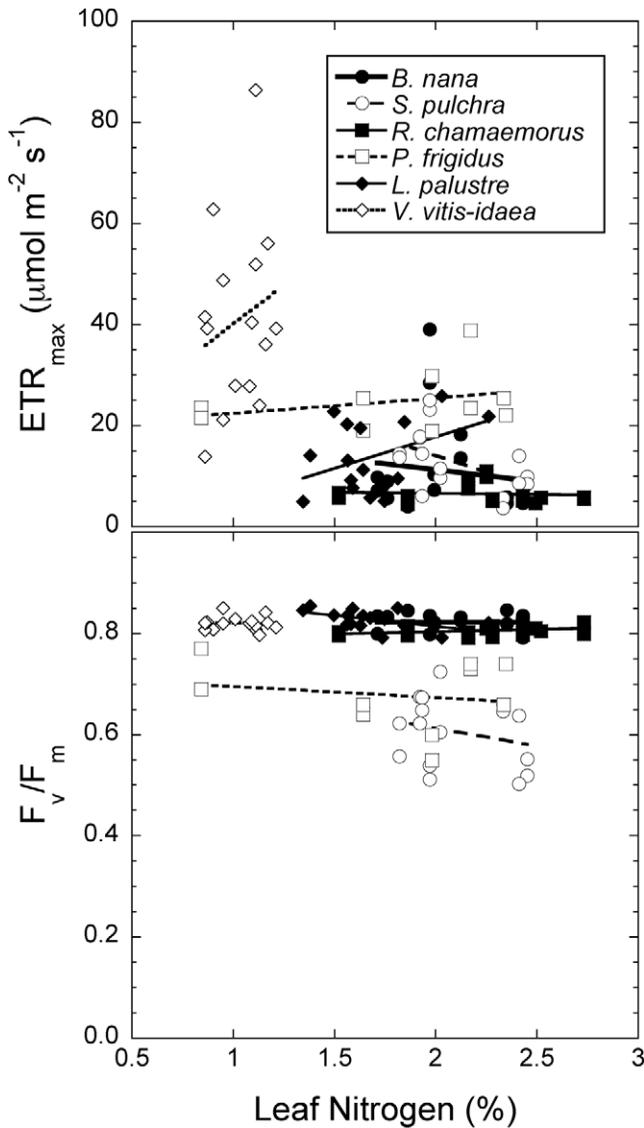


FIGURE 4. Relationship between maximum PSII electron transport rate (ETR_{max} , $\mu\text{mol electrons m}^{-2}$ leaf area s^{-1} ; upper) or PSII efficiency (F_v/F_m ; lower) and leaf nitrogen content (% total dry mass). Each point is the mean of 3 measurements taken for each species at 8 hill slope positions (5 positions for *Petasites frigidus*). A linear regression for each species is plotted; however, while these regressions were often significant, they rarely explain more than 5% of the variance in observed fluorescence characteristics.

shallow slope of the ETR_{max} vs. F_v/F_m relationship. Studies from acid mine tailings and other mineralized soils in Alaska show that *Salix* can accumulate very high levels of Mn and other trace metals (Gough et al., 2006). High trace metal concentrations can result in both reduced Rubisco activity (Kitao et al., 1997), and reduced PSII activity (Kitao et al., 1998), and research on other species from the genus *Salix* have also shown a strong influence of trace metals on F_v/F_m (Pietrini et al., 2010). Very little is known about the physiological ecology of *Petasites* and the cause for the lower F_v/F_m values, and the lack of distinct down slope trends in ETR_{max} are unknown. One interesting observation is that this is the only plant among the 6 species surveyed that is non-mycorrhizal and therefore may have a significantly different means of nutrient uptake (Hobbie and Hobbie, 2006).

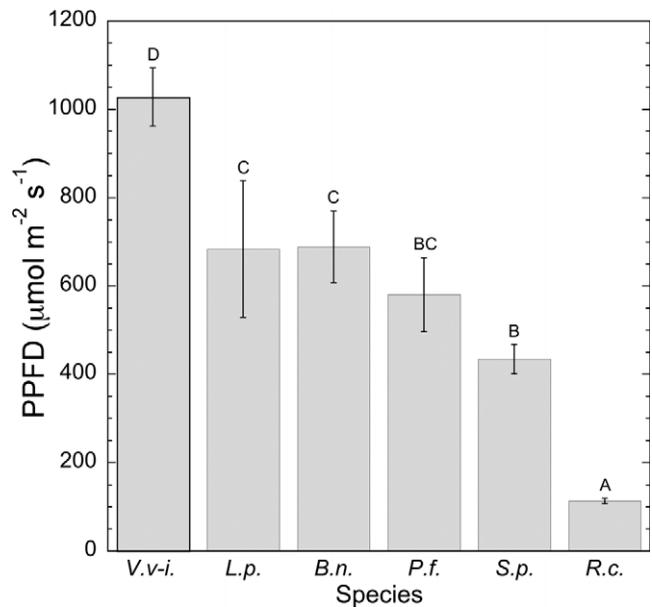


FIGURE 5. Photosynthetic photon flux density (PPFD) required to reach the maximum rate of electron transport (ETR_{max}) in 6 species sampled from the Imnavait Creek watershed. Each bar is the mean value derived from all rapid light response curves for each species ($n = 30$ to 42) and is subtended by the standard error of the mean. Species codes: B.n. = *Betula nana*, S.p. = *Salix pulchra*, R.c. = *Rubus chamaemorus*, P.f. = *Petasites frigidus*, L.p. = *Ledum palustre*, V.v-i. = *Vaccinium vitis-idaea*. Letters above individual treatment means are used to indicate a statistical difference at the $p < 0.05$ level of significance.

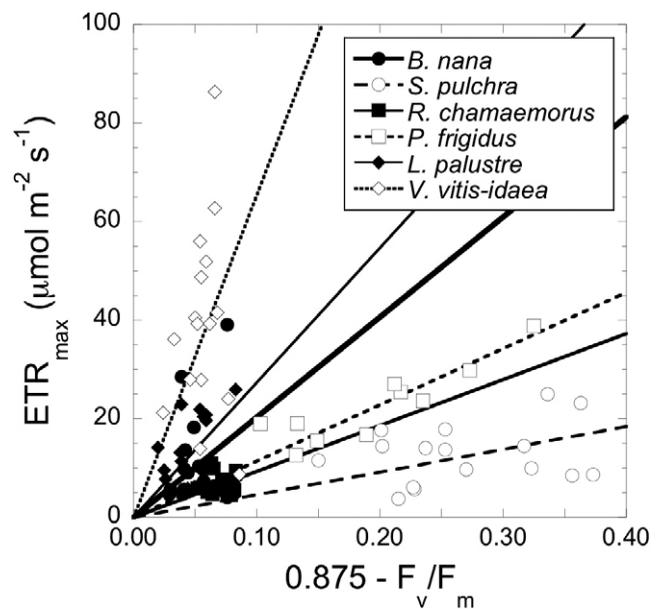


FIGURE 6. Relationships among PSII efficiency (F_v/F_m) and maximum PSII electron transport rate (ETR_{max}). Lines describing the relationship between relative efficiency of PSII and maximal rate of electron transport identify each of the six species (see text for further explanation of this relationship).

Leaf N concentrations were not a strong predictor of PSII activity among the various species and hill slope positions at Imnavait Creek. The lack of significant variation in leaf [N], particularly with hill slope position or between the WT and NWT locations may be responsible, despite a rather large overall range, from 1 to nearly 2.5% N. Still, though no significant differences were found at the leaf level, it is possible that N is primarily responsible for the gradient in productivity, as the LAI of the canopy was higher both down slope (peaking at location 6) and in the WT vs. NWTs (van Wijk et al., 2005; Kergoat et al., 2008). Furthermore the availability of specific N species (NH_4^+ vs. NO_3^- or amino acids) may have a significant impact on both the physiology and productivity of the various species at the various hill slope positions (Schimel and Chapin, 1996; McKane et al., 2002).

A decrease in the efficiency of PSII could occur from an increase in photoprotective energy dissipation, a decrease in photochemistry, or both (Kitajima and Butler, 1975). If photochemistry is involved it is logical to expect a concomitant decrease in the rate of electron transport at light saturation. Here we show this relationship holds and may reveal information about the shade tolerance of arctic species. Each of the 6 species fell on a distinctly different line when ETR_{max} was plotted against the dark-adapted F_v/F_m subtracted from the common intercept of 0.87. If 0.87 represents a theoretical maximum efficiency of energy conversion and electron transport through PSII via photochemistry in these species under ambient conditions, then the ordinate of this relationship would represent the loss of fractional efficiency. Thus, the relationship between this ordinate and the measured rate of ETR_{max} describes the ability of a particular species to continue to supply the needed electrons for carbon reduction even as photoinhibition reduced the maximum efficiency of PSII within the leaf. *Vaccinium* and *Ledum*, the two species with the highest light requirement to reach ETR_{max} , have the steepest slopes in this relationship, while *Salix* and *Rubus*, the two species with the lowest light requirement to reach ETR_{max} , have the lowest slopes. *Vaccinium* and *Ledum*, however, are also the two species with the weakest initial relationships between ETR_{max} and F_v/F_m , and *Vaccinium* did not intersect with the other 5 species at F_v/F_m of 0.87, suggesting caution may be required and that the strength of these relationships should be tested further.

Together the fluorescence data indicate that in these 6 arctic species there is a functional relationship between the maximum efficiency of light utilization by PSII and initial dark-adapted status of the reaction centers. Species with a larger spread of initial F_v/F_m values may have experienced the most photosynthetic stress over the landscape and as a result also have a lower spread in ETR_{max} . The only difference in the ordering of species between the light requirements for saturation of ΦPSII and the efficiency with which electron transport can continue with reduced PSII yield is a reordering of *Rubus* and *Salix*, the species with the consistently reduced F_v/F_m . The usefulness of this relationship, which may aid in the determination of relative light adaptation and investment in light harvesting, requires further evaluation.

The lack of increased rates of electron transport down slope or in the WT compared to the NWT locations suggests that physiological activity related to carbon gain is not responsible for the observed increases in plant biomass. Instead we concluded that

ecological considerations such as morphological plasticity and increased canopy nitrogen concentrations must be responsible for the observed changes in LAI and biomass accumulation. The impact of the strong reduction in ETR_{max} for carbon gain remains an open question, as does the precise reason for the observed reduction. We suggest that soil aeration, plant phenology, and Mn toxicity all deserve further study and that the causes and consequences of our observations be considered in the changing arctic landscape.

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